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THE BIOLOGICAL NATURE OF SOIL PRODUCTIVITY

by

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I start from the proposition that the aim of every organism which takes part in soil formation is to get the best living conditions for itself that the material environment will allow. That is easy to comprehend because it is the aim of every one of us, *Homines sapientes*, in making our own habitat, whether we are working in a laboratory, cultivating the land, making and spending money, or otherwise trying to enjoy ourselves. Neither a human society nor the far more complex society of the soil can exist in equilibrium unless a compromise, which satisfies no individual or species completely, can be established between the conflicting interests of the society.

It is commonly agreed that the so-called climax plant association with its associated fauna, in equilibrium with the climate, is the social organism which makes the fullest use of the environment; the plants and animals have made the best possible living conditions for themselves, and the productivity of the soil is then the highest possible under the prevailing conditions.

The invention of chemical fertilizers has, however, enabled us to raise the productivity of soil far above that attained under the climax association. Since the philosophical implications of this tremendous breakthrough of mankind have as yet scarcely penetrated into the realm of soil science, we shall confine ourselves here to considering the part played by the non-human soil population in making soil productive. I shall use the term soil *population* to include all plants, animals and micro-organisms which have any kind of contact with the soil, and the term *edaphon* to include only those organisms which make their homes mainly or entirely within the soil. The distinction is one of convenience only.

The population makes soil productive by transforming radiant energy into chemical energy by photosynthesis and heat-absorption by plants, using the plant material so produced as the energy source for animal and microbial life. A large part of the physical energy of the population is expended in securing suitable living conditions for itself in and on the soil. Whether a mole or worm is burrowing through the ground or making excrement, a seed germinating or a root growing, something is moving solid or liquid soil. Energy is being expended in making a habitat—a fertile soil.

The final result of this incessant movement, compression and distortion of the soil mass by uncountable organisms is a soil structure in which every surviving species can breathe, eat and drink. As Kubiena (1962) states, the cause of structure formation (*Formbildung*) is movement. Those parts of the population—the higher animals and subaerial parts of plants—that spend their lives above the soil surface provide much of the organic material which the soil-inhabiting parts use to fashion their abode. Soil fertility is a manifestation and measure of the success of the population in getting a high standard of living. Of two rather similar spruce forests, one may make a greater success of a podzol on a sedimentary than the other on a granitic substrate. The greater success of the one may be attributable to some property of the parent rock, or to a greater accession of solar energy, but both will produce podzols with similar horizons and structures.

A podzol is a comparatively unproductive soil with small faunal and microbial populations in its mineral horizons. The particularly sharp horizon differentiation of podzols can be largely explained on physicochemical grounds although the main chemical agent—humic acid—in podzolization is biological in origin. The small soil population can do little to improve its living conditions, and the non-exacting coniferous trees can thus maintain their dominance. It is perhaps significant that soils —e.g., podzol, solonets, solod—with sharp horizon differentiation are among the least suitable for dense and varied edaphons which could traverse horizon boundaries. Horizon formation is mostly abiotic. In more fertile soils, in which a crowding edaphon is packed into every nook and cranny, horizon boundaries are usually indefinite and diffuse. The tendency is for the edaphon as a whole to counteract unidirectional, inorganic forces such as gravitation.

The making of a soil structure out of structureless material involves two distinct but related processes—(1) the cementing of discrete particles to form aggregates, and (2) the shaping and orientation of the aggregates to form a macrostructure characteristic of the soil or of its separate horizons. The first is mainly a physicochemical process, and has been more studied than the second which is a biotic process for the study of which few, if any, available techniques are suited. In an unproductive soil such

as an alkali soil, structure is mainly the result of abiotic processes, in a productive soil it is mainly the result of biotic processes. The columnar structure of a solonets can be explained on physico-chemical grounds; the granular structure of a chernozem cannot. If the alkali is removed from a solonets and conditions become favourable for a steppe association, a chernozem structure will develop. The change in structure is not merely a matter of colloid flocculation and exchangeable bases. Flocculation can be achieved instantaneously in the laboratory; the build-up of a stable granular structure in the soil is a gradual process requiring the intervention of living organisms. Something like a granular structure can also be produced with soil conditioners—a human achievement which the future may rank with the invention of fertilizers as a milestone in man's conquest of the Earth.

We may liken the formation of soil structure to the building of a city. The bricks and stones and mortar, which vary from place to place as much as do the parent materials of soils but have much in common everywhere, are the abiotic parts of the city. The people who design the buildings and the communications between them are the biotic parts; without them a livable habitat could not be produced.

To continue the analogy. The parent rock provides the bricks; the whole population, in and on the soil, makes the mortar; the edaphon designs and builds the city, which is the soil.

The Role of Microbes

It is generally agreed that the structure associated with the most productive soils, and therefore most desirable for agriculture, is the crumb or granular type. Most studies on soil structure have been on crumb formation, and it has been shown that humic products are active agents in aggregation, and numerous data show a correlation between aggregation and humus content (Egawa & Sekiya 1956, Heinonen 1958, Lugo-López & Juárez 1959, Morel & Masson 1958).

Various organic constitutents, including humic acid, bacterial gums, polysaccharides and uronides, can aggregate soil particles into crumbs. Shrikhande (1936) was one of the first to establish the role of bacterial gums in aggregation, and Gel'tser (1943) showed that the products of autolysis of microbial bodies were active aggregating agents. Martin, Martin et al (1955) showed that the polysaccharide component of soil organic matter promoted aggregation. Chesters (1959) found that rapid decomposition of organic matter caused an increase in the quantity and size of aggregates in a silt loam, and that the increased aggregation was correlated with the polysaccharide content. Swaby (1950) got evidence that bacterial gums aggregated mineral particles in the gut of earthworms because the aggregates produced in worm casts from grassland soil were much more stable than those from arable soil which contained much fewer bacteria, but comparable numbers of other micro-organisms. Mehta et al (1960) found that artificial soil aggregates produced with polysaccharides were disintegrated by treatment with periodate which destroys polysaccharides, whereas natural soil aggregates were stable to periodate, but were disintegrated by ClO_2 which destroys lignin and humic acid. Greenland, Lindstrom & Quirk (1962) showed that in soils under permanent pasture, short-term pasture or cultivation, aggregates were resistant to periodate only when formed under permanent pasture. They suggested that the bonding agents in old pasture soils might be fungal hyphae and mycelia, or materials as yet unknown.

Fungal mycelia represent another microbial factor, besides bacterial gums and other humic products, that is active in binding soil particles together (Barratt 1962, Bond 1961, Gilmour, Allen & Truog 1949, McCalla 1945, McCalla & Haskins 1961, Martin et al 1959, Mishustin 1945). Mycelia vary widely in their binding capacity; Bond observed that dark-coloured mycelia were most persistent, and Martin et al that they were most resistent to decomposition. Any one filament, however, cannot persist for long, and it may be that fungal mycelia keep the soil in a temporary state of aggregation until some other agents stabilize the structure. Gel'tser (1943) asserted that the initial stages of (grass) decomposition were effected by fungi which were subsequently consumed by bacteria whose bodies produced "active" humus which could form colloidal organo-mineral compounds and bind the soil particles together. Chastukhin & Nikolaevskaya (1957) composted leaves with pure cultures of the fungus *Collybia dryophila*, adding fly larvae to some of the composts; the larvae rapidly destroyed the web-like white mycelia which had formed, and the decaying leaves were turned into a dark-coloured amorphous mass. Gilyarov (1953, cited by Chastukhin & Nikolaevskaya) calculated that 180 cubic metres of humus per hectare per annum were produced in a deciduous-forest soil by the excrement of collembola, mites and nematodes.

Whatever the actual process of humification, substances capable of glueing together particles larger than colloidal are produced.

Iimura & Egawa (1956) observed a great increase in water-stable aggregates when various soils were incubated in presence of glucose or plant residues. The greatest increase, during the first 16 days, coincided with a vigorous development of fungal hyphae. With the subsequent disappearance of the hyphae the larger aggregates decreased and the smaller aggregates increased in quantity, and the authors suggested that the binding effect of the hyphae was taken over by the cementing effect of bacterial gums.

The results described above suggest that while

bacterial gums, assisted by fungal mycelia, are the aggregating agents in the early development of a soil structure, the maturing and stabilizing of the structure are effected by the "aging" of the gums to humus and by the activities of organisms of all sizes shaping, compressing and penetrating the aggregates in their ceaseless efforts to make and maintain an environment in which they can exist.

*The Role of Macrobes**

While microbes produce the cement with which the ultimate particles are bound together, macrobes form (i.e., shape) the crumbs, cracks, crevices and pores which characterize the visible soil structure. All members of the macrobial edaphon take part in this all-embracing soil-forming activity, and at present only in a few cases can we identify a particular activity with a particular type of organism. For example, the role of grass roots in binding and compressing soil particles and penetrating the soil mass is universally recognized. That this, more than the humus produced by the vegetation, is the main factor in forming the typical grassland crumb structure is shown by the decline in aggregation that results as soon as grassland is plowed up (when humification is exceptionally intense) (Gel'tser 1943). The weak water stability of crumbs, observed by many workers, from cultivated as compared with grassland soil points also to a powerful effect of grass roots in creating structural stability (e.g., Emerson & Dettmann 1959). Evidence from the organically and inorganically fertilized plots of the Broadbalk permanent-wheat field at Rothamsted (1962) suggests that wheat roots are more effective than humus in maintaining or improving soil structure.

Klintworth & Naude (1954) obtained, over several seasons, a positive correlation between soil carbon content and water-stable aggregation under irrigated perennial grasses, and a negative correlation under annual crops. Grasses were the best aggregators, then maize and cowpeas, then lucerne. Klintworth & Naude stated that their results supported Gel'tser's theory that aggregate formation was brought about by the autolytic products of bacterial bodies. An alternative explanation could be that, under the conditions obtaining, most of the aggregation was done by roots pushing their way through the soil and using whatever colloidal cements were available to create conditions in which they could continue to live.

Larger and smaller roots than those of grasses do the same, and all leave their impress on the soil's structure. Graminaceous plants, however, are particularly effective in producing conditions of high productivity by making a porous crumb structure in which a large and varied edaphon can exist and which it can further modify to the advantage of its members. Productivity feeds on itself.

It may be justifiable to make the rather sweeping generalization that in the two great plant-ecologically distinguished worlds of the soil, the movement of plant roots is the major structure-forming factor in grassland soils, and the movement of animals in forest soils. It may be noted that, although the role of earthworms in helping to create the crumb structure of Russian chernozems has been accepted since the time of Dokuchaev, these animals do not commonly occur in North American prairie soils. Crumb-mull structure can be produced in grassland soils without earthworms, though they appear to be essential for its formation in at least temperate forest soils.

Of the macrofauna, most attention has been given to earthworms which are among the largest and agriculturally the most beneficial of the soil inhabiting fauna. Earthworms, together with other burrowing animals, have a considerable effect, though perhaps more transient than that of roots, on soil structure by making channels, but their most characteristic and most studied action on soil formation is their ingestion of mineral and plant materials at one end and their excretion of them as structured soil at the other. Earthworms have been described as "humus factories", but a more realistic description might be "soil factories", because in the worm's gut the whole process of biological soil formation, starting with mineral particles and fresh plant material and ending with fertile soil, seems to run its course. In particular, the union of mineral and organic matter to form the organo-mineral complex—a synthesis as vital to the continuance of life as, and less understood than, photosynthesis—occurs mainly inside worms and other soil-eating animals. As already mentioned, however, formation of structural mull is found in prairie soils from which earthworms are usually absent.

Meyer (1943) composted straw with additions of basalt meal and nitrogen fertilizer. A large population of earthworms and insects developed in the compost. At the end of two years about 75% of the compost consisted of worm and other excrement which, as a black, earthy, crumbly material, was easily distinguished from the brown, rotted-straw fragments which still retained their plant structure. The excrement had a C/N ratio of 10 and contained 65% ash, the rotted straw had a C/N ratio of 18 and contained 6.8% ash. There was evidence that a stable chemical union had taken place between the basalt meal and humic matter in their passage through the worms.

Spannagel (1960) described experiments on a sandy podzol (formerly under meadow) which was treated with manure and fertilizers, and agricultural crops were grown on it for 24 years. Plot I (pH 4.5) received no lime; plot II was limed to pH 5.8 and plot III was limed to pH 6.5. At the

*This word includes all fauna and flora that can be seen with the naked eye.

end of 24 years plot I showed a compact structure, no sign of mull formation, and organic matter distributed in particulate form, uncombined with mineral soil. Plot II showed a less compact structure, and a general humus colouration produced by "brown humic acids" which do not form organo-mineral complexes. Plot III showed a well developed water-stable structure of black crumbs; there was much animal excrement in the soil. Earthworms were abundant in plot III, but not in the others, and appeared to be the prime agents in structure formation, though the very formation of a crumb structure had promoted the development of an active faunal and microbial population. A crumb structure was also produced in the excrement of worms which had been introduced with plant material into a pure coarse sand (Spannagel 1954). Thus worms seem able to make an organo-mineral complex out of quite large mineral particles.

A large part of the amorphous organic matter of soil is composed of excrement produced by members of the soil fauna. Excrement is presumably an unstable form of humus that changes, by microbial action, into more stable forms. Barratt (1962) found that much of the organic matter in recently colonized coastal sand dunes consisted of faecal pellets from mites and collembola, the pioneer fauna of the dunes. The pellets, assisted by fungal hyphae, seemed to stick the sand particles together into primitive aggregates.

Franz (1950) classified the edaphon as edaphon *sessiles*, *natantes*, *serpentes* and *fodentes*—or, in English, stay-putters, swimmers, crawlers and burrowers. The first three classes, including all the micro- and many of the meso-fauna and flora, have little direct effect on physical structure, because they find living space in already existing crevices, channels and pores, but they have an indirect effect in providing the materials—gums, excrement, nutrients—which the burrowers (roots, rodents, worms, ants, larvae, etc.) use to fashion their abodes and communication system. Many burrowers eat soil particles in order to facilitate their passage, and thereby bring about the union of organic and mineral matter that is the unique chemical reaction of soil formation.

Conclusion

In the foregoing I have tried to show that soil fertility is a biophysical rather than a physico-chemical phenomenon. It concerns the transformation of energy in living organisms; essentially the transformation, in plants, of heat and light into chemical energy which is returned to the soil to provide energy for the edaphon to live and *work* to construct a habitat. The physical work performed by the edaphon in moving through soil, in compressing or expanding peds, and in passing material through their bodies is the main action in the formation of the structure associated with a fertile soil.

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